BEHAVIORAL RESPONSES OF MIGRATING BIRDS TO DAYLIGHT AND DARKNESS: A RADAR AND DIRECT VISUAL STUDY

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In spring nearly all the passerine migrants that enter southern Louisiana do so after completing a migration across the Gulf of Mexico, and although most of the birds are considered nocturnal migrants and embark on their crossing at night (Lowery, 1951), they usually arrive on the northern Gulf coast during the daytime (Lowery, 1955; Newman, 1957). The migrants that arrive during the day alight shortly after reaching land and usually initiate another migration the same night, but occasionally the trans-Gulf flights continue to arrive after nightfall (Gauthreaux, 1968, 1971). Because of the timing of these movements, I have been able to examine the landing behavior and the altitudinal and spatial distribution of the same population of migrants aloft during the day and at night.

MATERIALS AND METHODS

This paper is based on radar, direct visual, and acoustic methods which are essentially the same as those given in earlier papers (Gauthreaux, 1969, 1970, 1971). I gathered data from the WSR-57 radar and made telescopic watches at Lake Charles and New Orleans, Louisiana, during spring migration from 1965 to 1967 and accumulated information on the landing behavior of the trans-Gulf migrants on the Louisiana coast from 1958 to 1968 (see Newman, 1958; Newman and Lowery, 1959). Call-notes from migrants aloft were counted during daytime and nighttime telescopic watches throughout the study.

DAYTIME FLOCKING

The data I collected with a telescope and binoculars indicate that the majority of passerines arriving from over the Gulf during the daytime were in compact flocks. Although isolated passerines were frequently recorded, the total number of birds in flocks exceeded the total number of single birds by a factor of three. The aggregations of small and medium sized passerines ranged from two or three individuals to more than 100; the average was 20. The largest flock I saw with the telescope was 175 birds, and the largest flock I recorded with binoculars was 300 birds.

The migrants were in four basic flight formations. About 70 per cent of the flocks were nearly circular or slightly oval in shape. About 30 per cent were in a line formation; in 20 per cent the line was perpendicular to the flight direction, and in the remaining 10 per cent it was parallel to the flight direction. On two occasions the migrants appeared to be randomly spaced,

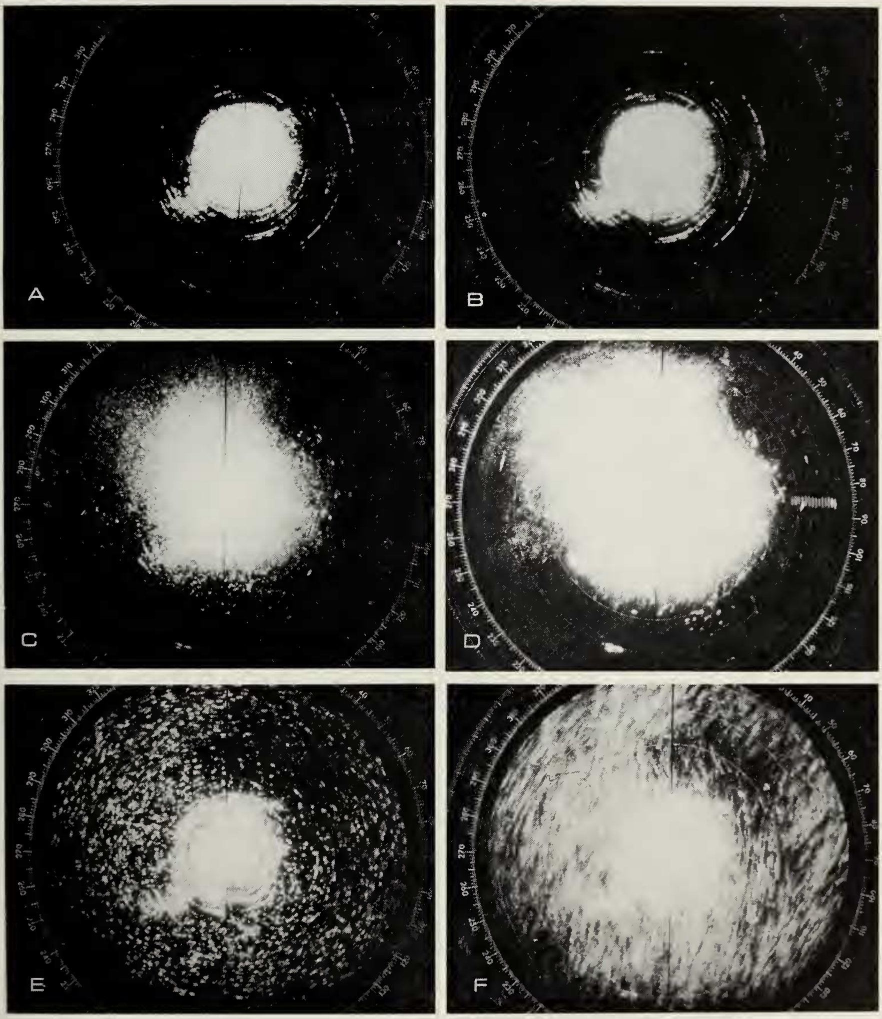

FIG. 1. Photographs of the radar screen at Lake Charles, Louisiana, during spring of 1965. A, C, and E are exposures for a single revolution of the antenna; B, D, and F are five-minute time exposures. A and B—19 March, 23:28 to 23:33 CST, 4° antenna elevation, no migration. C and D—15 May, 20:11 to 20:16 CST, 3° ant. elev., nocturnal migration. E and F—15 May, 18:46 to 18:51 CST, 3° ant. elev., daytime migration.

but this could have resulted from several large flocks joining together. The following example illustrates the compactness of the flocks. On the afternoon of 7 May 1965 two flocks of 30+ and 15+ passerines passed through the field of the vertical telescope when a partial moon was located in the field of view. From each flock 12 and seven birds, respectively, were over the lunar background at the same time.

Figures 1A and 1B show the radar screen (PPI) of the WSR-57 at Lake Charles, Louisiana, when there was no migration. The permanent echoes in the middle of the radar screen are from ground objects in the vicinity of the radar installation and are present in the other radar photographs. The echoes on the PPI from arriving trans-Gulf migrants were coarse bright dots (Figures 1E and 1F). They were strong and persistent and could be tracked for distances of two to six nautical miles. Finer echoes were often distributed among the larger ones, and frequently several coarse echoes coalesced on the radar screen. Although the density of the dot echoes occasionally caused saturation of the PPI (large areas of solid echo coverage), the concentrations were usually such that separate echoes were distinguished and counted.

By employing the radar's attenuation circuits and reducing signal strength, I estimated the relative abundance of different flock sizes. Forty-five per cent contained 12 birds or fewer; 55 per cent contained 13 to 200+ birds, and the median flock size was 19 birds. The earliest that I saw radar echoes from trans-Gulf migrants offshore was 41 minutes before sunrise, and the echo pattern suggested that the birds were already flocked.

LANDING BEHAVIOR

In favorable weather (clear to partly cloudy skies and southerly winds), most flocks of trans-Gulf migrants passed over the first coastal woodlands with only a few birds dropping out and alighting; the majority continued farther inland to the first extensive forests. When rain and adverse winds were present over the Gulf, or the Louisiana coast, or both, many more individuals landed in coastal woodlands. Under these conditions entire flocks often plummeted from great heights into the trees. When viewed through binoculars from one end of a wooded ridge, the migrants looked like large, dark hailstones falling into the trees.

The following sequence of events characterizes the landing behavior of the migrants as diagramed in Figure 2. As a flock high aloft moved over a coastal woodland some of the individuals hesitated, hovered, or flew in broad, shallow spirals while the remaining flock members continued farther inland. The individuals that left the flock then closed their wings and dove nearly straight down. Diving at great speed the migrants occasionally braked their descent by quickly flitting their wings, and just above the trees they abruptly pulled out of the dive producing a distinct whizzing sound. The birds then continued flying rapidly for 10 to 50 feet and landed with a quick flutter of their wings. After alighting the birds often remained motionless for two or three minutes, and then preened for two or three additional minutes. The

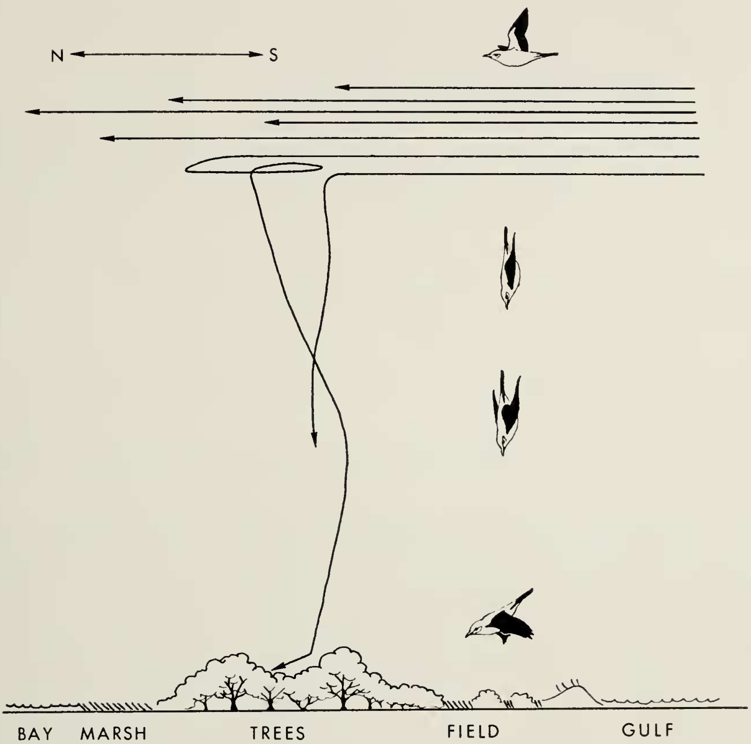

FIG. 2. Daytime landing sequences of trans-Gulf migrants in a coastal woodland. The bird postures figured on the right side are adopted during the landing behavior.

grounded migrants then started to feed, and many of the birds while moving from tree to tree continued in the direction of their migration.

When observed through the vertical telescope certain of the flocks aloft appeared to be aggregations of a single species, and I verified this on those occasions when entire flocks dove into the trees. I recorded the following species in homogeneous species flocks: Eastern Kingbird (*Tyrannus tyrannus*), Catbird (*Dumetella carolinensis*), Wood Thrush (*Hylocichla mustelina*). Red-eyed Vireo (*Vireo olivaceus*), Tennessee Warbler (*Vermivora peregrina*). Yellow Warbler (*Dendroica petechia*). Bay-breasted Warbler (*Dendroica castanea*), Bobolink (*Dolichonyx oryzivorus*). Orchard Oriole (*Icterus spurius*), Baltimore Oriole (*Icterus galbula*). Scarlet Tanager (*Piranga olivacea*), Summer Tanager (*Piranga rubra*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Blue Grosbeak (*Guiraca caerulea*). Indigo Bunting (*Passerina cyanea*), Painted Bunting (*Passerina ciris*). and Dickcissel (*Spiza americana*). In addition, some flocks contained only one sex (e.g.. Baltimore

TABLE 1

ALTITUDE OF DAYTIME MIGRATION AT LAKE CHARLES AND NEW ORLEANS
(Expressed as percentage of total number of dot echoes aloft)

Antenna elevation		Altitudinal zones in feet				
2.5°		*796–1,859*	*1,592–3,718*	*2,388–5,577*	*3,184– 7,437*	*3,980– 9,296*
(N = 4)	$\bar{x}$	8	11	30	36	15
	S.D.	7	3	10	3	14
3.0°		*1,061–2,125*	*2,123–4,251*	*3,184–6,377*	*4,246– 8,503*	*5,307–10,629*
(N = 30)	$\bar{x}$	5	10	29	38	18
	S.D.	6	5	10	11	12
4.0°		*1,593–2,659*	*3,186–5,319*	*4,779–7,979*	*6,373–10,638*	*7,966–13,298*
(N = 9)	$\bar{x}$	5	15	35	35	10
	S.D.	3	8	13	16	10

Oriole, Scarlet Tanager, Rose-breasted Grosbeak, Blue Grosbeak, Indigo Bunting, and Painted Bunting). It was often difficult to detect homogeneous species flocks once the birds landed and fed together in the trees. I did notice frequently that certain species were more abundant in certain portions of a particular woodland and that the relative abundance of a particular species differed markedly among different coastal woodlands. Two species of herons, the Green Heron (*Butorides virescens*) and the Yellow-crowned Night Heron (*Nyctanassa violacea*), showed the same landing behavior as the landbirds, and both of these species were commonly found resting in trees after completing a trans-Gulf migration.

ALTITUDE OF DAYTIME AND NIGHTTIME FLIGHTS

Table 1 gives the altitudinal distribution of the trans-Gulf migrants during their daytime arrival at the latitude of the Lake Charles and New Orleans radar stations (30°N). I gathered the data by counting dot echoes on the radar screen in a 5 × 5 nautical mile area centered at 5, 10, 15, 20, and 25 nautical mile range. The numbers of dot echoes were averaged for each altitudinal stratum and were corrected for increasing beam size and loss of power that follows the fourth power rule (see Eastwood, 1967).

On Lake Charles radar the altitude of the daytime movements averaged approximately 500 feet higher over land than over the Gulf, and flights were frequently 1,000 feet higher over New Orleans than over Lake Charles. The reason is probably that the migrants rather consistently flew above the convective cumulus clouds that formed near the coastline and piled higher as they moved inland with southerly winds. The cumulus over New Orleans

TABLE 2

ALTITUDE OF NIGHTTIME MIGRATION AT NEW ORLEANS
(Expressed as percentage of total number of birds aloft)

Antenna elevation		Altitudinal zones in feet			
2.5°		*796–3,718*	*1,592–5,577*	*2,388–7,437*	*3,184–9,296*
(N = 34)	$\bar{x}$	70	20	8	4
	S.D.	19	13	10	8
		796–1,592	*1,592–2,388*	*2,388–3,184*	*3,184–3,980*
(N = 30)	$\bar{x}$	74	18	7	2
	S.D.	17	14	8	3

were better developed than those over Lake Charles because the former city is farther inland than the latter, and the cloud formations had more time to build up, inducing the birds to fly higher. Whenever cumulus development exceeded 7,000 feet the migrants lowered their altitude. The distribution of the daytime flights was frequently the same as the altitude of the inversion layer aloft, but cumulus rarely develop above the altitude of an inversion. The air just above an inversion is quite stable and flows smoothly, and Raynor (1956) has suggested that migrants might prefer to fly in this zone.

Excluding cirrus overcast, solid overcast covered southern Louisiana on 11 days when trans-Gulf flights arrived. On nine of these days the mean altitude of the overcast base was 2,540 feet (S.D. = 1,160 feet; range = 1,300 to 5,000 feet), and 80 to 95 per cent of the migrants displayed on radar were above the overcast. Only on two days when the base of the overcast was at 7,500 feet and 10,000 feet did most of the migrants fly below the cloud layer. On 30 April 1967 cumulus cloud tops (8/10 coverage) extended up to 3.100 feet and the base of a higher cloud layer (9/10 coverage) was at 10,000 feet. On this afternoon 83 per cent of the migrants passing over the radar station flew between 4,000 and 6,000 feet between the cloud layers. On certain occasions some migrants appeared to be flying in clouds. Three times with binoculars I saw flocks of migrants so close to the base of a cloud that some individuals in the flocks momentarily disappeared into the cloud.

Whenever migrants continued to arrive from over the Gulf and pass over the radar stations near nightfall, their height lowered markedly. The average change from the daytime altitudinal distribution to the nighttime one was approximately 3,000 feet. Table 2 gives the quantity of nocturnal migration per altitudinal stratum expressed as the percentage of the total number of birds aloft. These data are from New Orleans during the spring of 1967, and I gathered them by using the attentuation technique (Gauthreaux, 1970). The data were corrected in the same manner as the daytime data, but they refer to densities of individual birds and not flocks. Seventy per cent of the migrants at night were most frequently between 796 feet and 3,718 feet. Within this zone approximately 75 per cent were between 796 feet and 1,592 feet.

Excluding cirrus overcast, solid overcast over southern Louisiana occurred on 5 nights of migration. The altitudes of the solid cloud layers on three of the nights were 2,800; 8,000; and 9,000 feet, respectively, and the migrants were below the overcast. On the remaining two nights the overcast was at 1,000 and 900 feet, and the migrants were in and above the cloud layer. Call-notes from the migrants on the latter two nights were quite numerous (50 to 100 per minute).

I recorded nocturnal flights at altitudes much higher than usual on 2 May and 4 May 1967. On 2 May, 42 per cent of the migrants were between 5,580 and 7,440 feet; on 4 May, 41 per cent were between 3,720 and 5,580 feet. When these altitudes were compared with the winds aloft (radiosonde-radar tracked balloon) for these nights, the migrants were found to be flying with favorable winds in warmer air above shallow cold fronts and northerly winds that had moved into the area.

CHANGE IN FLOCKING BEHAVIOR AT NIGHTFALL

As the altitude of migration lowered near nightfall another feature of the migration also changed—the flocks characteristic of daytime migration disbanded. On 11 occasions during full moon periods, I observed by moon-watching the breakup of flocks as trans-Gulf migrants continued to arrive over the Louisiana coast near sunset and later. The moon rises before sunset on the days preceding the full moon and it rises at the time of sunset on the date of the full moon. I began the watches while it was still daylight, and the passerine migrants that crossed the moon were still in tight aggregations with up to 10 birds against the moon at one time. As the watches continued and darkness approached the aggregations became looser, and shortly after dark only single birds passed before the lunar background. On five of these occasions thin cirrus cloud veiled the moon and the entire field of the telescope could be used to see the silhouettes of the migrants. Even with the added field of view only *single* landbirds were seen once it was night. After dark the ducks and shorebirds that passed before the moon were clearly grouped into tight flocks.

On the radar screen from the time of sunset to the time of darkness the large dot echoes characteristic of daytime migration changed to a finely stippled echo pattern. The fine dust-like echoes on the PPI of the WSR-57 are typical of nocturnal migration when passerine birds are flying singly in the night

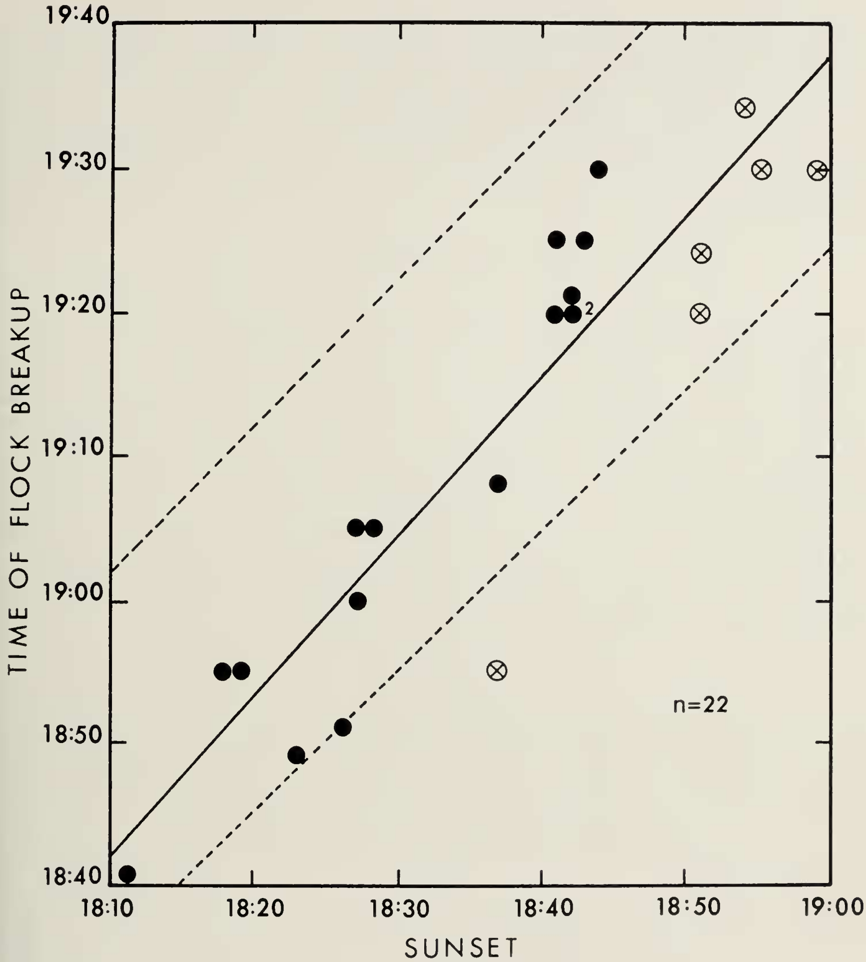

FIG. 3. Scatter diagram showing the time of the breakup of daytime flocks. Upper and lower dashed lines represent the end of nautical and civil twilight, respectively. The solid line is the computed line that best fits the points. The solid circles are points for New Orleans and the crossed circles are points for Lake Charles.

sky (Figs. 1C and 1D). The flock echoes on radar started to disband about 26 to 46 minutes after sunset. The mean time of the start of flock breakup based on 22 cases is 35 minutes after sunset with a standard deviation of 5 minutes. Most of the dot echoes were completely fragmented about 15 minutes later, or after the end of civil twilight and the beginning of nautical twilight. The duration of civil twilight during spring migration at 30°N is 24 to 25 minutes, and it is followed by nautical twilight which lasts for 52 to 59 minutes from 19 March to 19 May. Figure 3 is a scatter diagram showing the time of flock breakup in relation to the time of sunset and the beginning of nautical twilight. The breakup of passerine flocks aloft occurs about the same time as the exodus of grounded trans-Gulf migrants from the woodlands of southern Louisiana (Gauthreaux, 1971), and both events are clearly distinguishable on the radar screen.

CALLING BY MIGRANTS ALOFT

If trans-Gulf migrants flying high overhead during the day called, I did not hear them. However, when migrants were alighting in coastal woodlands during the day, they often gave call-notes. Passerine migrants called infrequently even when flocks aloft were disbanding and migrants were departing from woodlands during the first part of the night under fair skies. In contrast, I counted many call-notes from songbirds early in the evening on overcast nights and when trans-Gulf migrants were arriving after dark and landing. The greatest amount of calling from passerines usually occurred when the radar showed the density of migration to be falling rapidly. Shorebirds and waterfowl normally called frequently after dark and throughout the first half of the night.

DISCUSSION

Lowery (1951) established that nocturnal passerine migrants cross the moon individually as they initiate their trans-Gulf migration from areas south of the Gulf of Mexico. In this paper I have emphasized that these nocturnal migrants arrive from over the Gulf on the northern coast during the daytime in flocks. How single birds over the Gulf manage to congregate into homogeneous, single-species flocks is an intriguing question that is not easily answered. The radar findings of Gehring (1963) on daytime autumn migration in northern Switzerland suggest that the grouping possibly takes place at dawn. He found that the initial phases of diurnal migration occurred about half an hour before sunrise and at that time the radar echoes from the migrants were small and diffuse—an echo pattern characteristic of nocturnal migrants flying indvidually. As the light intensity increased the echoes became larger probably due to a tendency of the birds to form larger flocks. It is possible that nocturnal passerine migrants when forced to continue migrating in daylight over the Gulf of Mexico show the same flocking behavior exhibited by typical diurnal migrants at dawn. The two types of migrants show additional similar behaviors.

Gehring (1963) discovered that the altitude of migration over northern Switzerland decreased until half an hour before sunrise when it increased sharply. He attributed the lowering phase to nocturnal migrants ending their migration and the sharp increase to diurnal migrants. Myres (1964) recorded a late-night descent of nocturnal migrants flying over the southern part of the Norwegian Sea and the northern part of the North Sea, but near dawn the migrants gained altitude quickly. Although my evidence is circumstantial, nocturnal migrants probably show a gain in altitude at dawn over the northern Gulf, for the altitude of daytime migration from over the Gulf is approximately 3,000 feet higher than that typical for nighttime migration in the same area. Unfortunately, at the critical time when the ascent behavior occurs most of the migrants are too far offshore to be detected by coastal radar.

Lowery (1951) and Lowery and Newman (1955) found that most passerines aloft at night migrate singly and are randomly spaced. Nisbet (1963*a*) concluded that "... migration in small groups is a habit widespread in at least three North American families, Parulidae, Turdidae and Emberizidae, as well as in non-passerines." He pointed out that it would be valuable to seek direct visual evidence for the shape and size of groups by observing either when the moon is very low, or when haze or thin clouds cover the moon and a relatively large area of the sky can be examined with a low-power binocular. My telescopic and binocular observations under the latter conditions do not support Nisbet's conclusions. I found that daytime flocks of passerines disband at dusk; shorebirds and waterfowl remain in flocks. The change in echo pattern on the radar screen of the WSR-57 further supports the conclusion that most nocturnal passerine migrants fly individually in the night sky. According to the evidence presented by Eastwood and Rider (1966) some of the echoes on radar at long ranges are probably true groups of nocturnal migrants similar to those found by day; others, and perhaps the majority, are pseudo-groups which are a consequence of the pulse-volume effect (poor radar resolution) particularly with 23- and 10-cm radars. Schaefer (1968) also found by careful analysis of radar signals from migrating birds that the majority of nocturnal migrants over central England fly singly. Furthermore, when passerine migrants initiate their flight from woodlands at the beginning of the night they do so individually and not in groups (Hebrard, 1971).

The altitude of migration lowered during twilight whenever trans-Gulf migrants continued to arrive from over the Gulf near nightfall. Bellrose and Sieh (1960) described a similar phenomenon in flocks of migrating ducks. They recorded a gradual descent of birds from 2,000 or more feet to 500 feet as darkness approached on an overcast afternoon and believed that the ducks were attempting to remain in visual contact with the ground. This behavior should be looked for at other locations where nocturnal migrants are required to fly over 24 hours without landing. The lowering of the altitude at nightfall does not appear to be related to landing, for the number of migrants aloft usually increased after the descent as grounded migrants started their migration. The average altitude of nocturnal migration that I recorded from southern Louisiana is lower than that reported by certain workers (e.g., Lack, 1960; Nisbet, 1963*b*; Bellrose and Graber, 1963), but it is very close to other published figures (e.g., Eastwood and Rider, 1965; Able, 1970; Bellrose, 1971).

During the day the altitude of migration gradually increased as migrants crossed the coastline and moved inland. Similar altitudinal differences over land and sea have been reported by Bergman and Donner (1964) and Eastwood and Rider (1965). The propensity of trans-Gulf migrants to gradually gain altitude after crossing the coast is probably a response to stay above the building cumulus over land. Despite the increase in altitude, most birds landed when they reached the first inland forests. Although my data are few, it appears that migrants fly above overcast during the day when the cloud layer is under 7,000 feet. At night when solid cloud cover is above 3,000 feet, most migrants are below it, but when the overcast is lower most migrants fly in or above the cloud.

Graber (1968) reported that nocturnal migrants normally call more frequently later in the night reaching a peak in the pre-dawn hours. He also found that cloud cover causes a sharp increase in the number of call-notes. In southern Louisiana during the first part of the night, flight calls from passerine migrants aloft were scarce unless the birds were landing or it was overcast. When my radar and telescopic observations revealed that the density of nocturnal migration was declining rapidly, calling by the migrants was greatest. Hebrard (1971) found that nocturnal migrants did not call when they initiated their flights from woodlands in coastal Louisiana. Similarly, I did not hear flight calls when the daytime flocks disbanded at nightfall. Waterfowl and shorebirds called frequently at the beginning of the night even under clear skies. That calling serves some function in flock maintenance cannot be disputed, but it also seems plausible that calling by passerine migrants at night functions in some manner in the landing process. Exactly what that function is will require further investigation.

SUMMARY

I studied the behavior of migrating birds aloft by means of telescopic and binocular observations during the day (open sky overhead) and at night (ceilometer and moon-watching) and with WSR-57 radars in southern Louisiana. Spring passerine migrations across the Gulf of Mexico usually arrived on the northern Gulf coast during the daylight hours, and most of the birds were in tight flocks that averaged about 20 birds. On radar the flocks produced coherent dot echoes, and most occurred at an altitude of 4,000 to 5,000 feet (1,220 to 1,524 meters). When landing the migrants dove nearly

straight down from these altitudes and produced a whizzing sound as they pulled out of the dive just above the trees.

The daytime flocks of passerines disbanded about 30 to 45 minutes after sunset, and the altitude of the migration lowered approximately 3,000 feet (915 meters). At night individual passerines produced fine, dust-like echoes on the radar screen while flocks of waterfowl and shorebirds contributed the scattered dot echoes. Most nocturnal migration occurred between 800 and 1,600 feet (244 to 488 meters). Flight calls from migrants were heard during the day when the birds were landing. Passerine calling at the beginning of the night was primarily associated with landing and overcast. Waterfowl and shorebirds called regularly during the first part of the night even under clear skies. Calling by migrants aloft probably serves to keep individuals of a flock together and functions in the landing of songbird migrants at night.

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